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**Stress hormones, social associations and song learning in
zebra finches**

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19 The use of information provided by others is a common short-cut adopted to inform decision-
20 making. However, instead of indiscriminately copying others, animals are often selective in what,
21 when, and whom they copy. How do they decide which “social learning strategy” to use? Previous
22 research indicates that stress hormone exposure in early life may be important: while juvenile zebra
23 finches copied their parents’ behaviour when solving novel foraging tasks, those exposed to elevated
24 levels of corticosterone during development copied only unrelated adults. Here we tested whether
25 this switch in social learning strategy generalises to vocal learning. In zebra finches, juvenile males
26 often copy their father’s song; would corticosterone-treated juveniles in free-flying aviaries switch to
27 copying songs of other males? We found that corticosterone-treated juveniles copied their father’s
28 song less accurately as compared to control juveniles. We hypothesised that this could be due to
29 having weaker social foraging associations with their fathers, and found that sons that spent less
30 time foraging with their fathers produced less similar songs. Our findings are in line with a novel
31 hypothesis linking early-life stress and social learning: early-life corticosterone exposure may affect
32 social learning indirectly as a result of the way it shapes social affiliations.

34 Keywords: developmental stress, information use, social networks, social learning, song learning,
35 stress hormones



36 INTRODUCTION

37 While most studies of learning and cognition are conducted on subjects in social isolation, most wild
38 animals live in a social context – be it a territorial or a gregarious one. Animals use information
39 generated by the behaviour of others in species ranging from fruit flies (*Drosophila melanogaster*)
40 [1] to humans [2]. Social information can shape individuals’ decisions when tackling virtually every
41 life challenge, from learning to exploit novel food sources [3] and choosing mates [4], to avoiding
42 brood parasites [5] and predators [6]. However, theory suggests that indiscriminate social
43 information use is not adaptive [7], and accumulating evidence shows that animals employ “social
44 learning strategies” in choosing what, when and whom to copy [8,9]. Yet individuals vary in whether
45 they (appear to) use social information [10] and, if so, in which social learning strategy they adopt
46 [11]. Relatively few studies have investigated the mechanisms underlying this inter-individual
47 variation in social information use, but there is accumulating evidence to suggest that early-life
48 conditions [12,13] and social interactions [11,14–18] may be important.

50 In two recent studies, we investigated how early-life conditions shape social associations and social
51 learning strategies in the highly gregarious zebra finch (*Taeniopygia guttata*). First, we found that
52 juvenile zebra finches that were fed the avian stress hormone corticosterone during the nestling
53 phase later formed less exclusive (or more random) social bonds in a colony setting (free-flying
54 aviaries containing 6-7 families) relative to their control-treated siblings. In particular,
55 corticosterone-treated juveniles spent less time foraging with their parents [19]. When presented
56 with a novel foraging task, we next found that while control juveniles tended to copy their parents’
57 behaviour to solve the task, their corticosterone-treated siblings exclusively copied unrelated adults
58 [20]. This could be because the corticosterone-treated juveniles may not have perceived their
59 parents as desirable role models, or because the parents may have treated their experimentally
60 stressed (and thus “lower quality”) offspring differently. Regardless of the underlying mechanisms,
61 early-life corticosterone exposure appeared to induce a switch in with whom juveniles affiliated [19]

and who they copied when socially acquiring novel foraging behaviours [20]. The aim of the current study was to determine whether early-life corticosterone exposure had a similar effect on the social learning of song. If so, we wanted to identify whether this was due to corticosterone-associated changes in the choice of whom to copy, or a by-product of changes in social affiliation patterns. Bird song is the quintessential example of a socially transmitted trait, and song learning is likely to be important for individuals' fitness: which song an individual sings and how accurately they learn it can have long-lasting consequences for their later ability to compete in territorial disputes or court potential mates [21–23], and can predict individuals' reproductive success and longevity [24].

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In addition to potentially affecting social affiliations and/or song model choices, early-life stress may also influence song learning by impacting cognitive ability. Song learning involves a variety of cognitive processes. Juveniles typically acquire information about species-specific song by listening to the songs of adults ("tutors") during a relatively short period (the "sensitive window/phase") in development. They then memorise this information, often for many months, and use it to shape and practise their own song as they mature [25]. Studies that subjected juvenile songbirds to a variety of early-life stressors (e.g. increased brood size, food restriction, corticosterone administration; reviewed in [26]) often found that stressed males sing lower-quality songs; their songs tend to be shorter, contain fewer (unique) songs or syllables, less accurately copied syllables or syntax, and are perceived as less attractive by females. Some developmental stress studies even report a reduction in the volume of the song control nuclei in the brain [26] (see [27] for another example of environmentally-induced changes in brain morphology). The "developmental stress hypothesis" proposes a potential explanation for these findings [26,28]: song control nucleus development in the brain requires considerable energetic resources during a period of rapid physical and neuronal growth. If these energetic resources are constrained by developmental stressors such as sibling competition, food scarcity or predation threat, then song development is likely to be negatively affected. However, the juvenile males in these developmental stress studies, as in most captive

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3 88 studies on song learning, tend to be experimentally constrained to learn from a single adult tutor. It
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5 89 thus remains to be established whether developmentally stressed males show impoverished song
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7 90 learning in more naturalistic social contexts, such as in colonies where young birds are free to
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9 91 choose to associate with and learn from multiple potential song tutors. The importance of bi-
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11 92 directional interactions between the social environment and cognitive performance is now
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13 93 becoming more widely appreciated [29], and evidence for a critical influence of social context on
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15 94 cognitive performance is accumulating in species ranging from pond snails (*Lymnaea stagnalis*) [30]
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17 95 to Australian magpies (*Cracticus tibicen dorsalis*) [31].
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20
21 97 Zebra finches are the foremost model system for studies of song development [32–34]. Male zebra
22
23 98 finch song structure and performance play a crucial role in female mate choice in captivity [35] and
24
25 99 predict reproductive success in the wild [36]. Males repeatedly sing a single stereotyped and unique
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27 100 song motif during courtship. Captive studies suggest that juvenile males tend to learn these
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29 101 courtship songs from their fathers, if the latter are available as tutors during the sensitive phase
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31 102 when song templates are acquired, i.e. between ca. 35–65 days post-hatching, after they have
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33 103 fledged [37–40]. Zebra finches are also highly gregarious, non-territorial birds that breed in colonies
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35 104 ranging in size from ca. 4 to 136 pairs [41], making them ideal for studying song learning strategies in
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37 105 a dynamic social context. Even so, most experimental studies on zebra finches in captivity have been
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39 106 based on constrained song tutor choice: birds were usually confined to small cages and only given
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41 107 the choice to copy the song of their father or one alternative tutor, without the opportunity to freely
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43 108 associate in a broader social group. The two studies in which breeding pairs and their offspring were
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45 109 kept in free-flying aviaries containing multiple potential tutors [42,43] generated complementary but
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47 110 contradictory findings: Williams (1990) found that the majority of juveniles produced songs that did
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49 111 not resemble their father’s, and they instead appeared to copy the unrelated males that they
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51 112 interacted with the most. Similarly, Mann and Slater (1995) found that most juveniles learnt their
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53 113 songs from the male with whom they maintained greatest proximity, but in contrast to Williams
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(1990), this was often the father. These studies suggest that there could be considerable variation in the choice of song tutor under (semi-) natural rearing conditions, which is likely related to the social associations that young birds experience, and thus their social preferences. Here we take advantage of being able to quantify fine-scale social associations among all individuals in replicated colonies of zebra finches, combined with experimental manipulations of early-life conditions, to uncover some of the mechanisms that may underlie the observed variation in song tutor selection.

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In the current study, we examined the relationships between early-life exposure to corticosterone, fathers' and sons' social associations, and sons' song tutor choice and song copying accuracy. We used data from the same zebra finches and experimental design as in our previous studies [19,20]: half of the offspring in each of 13 zebra finch families were exposed to experimentally elevated levels of corticosterone in the nest. After fledging, all individuals' feeder visits in two aviaries were recorded using an automated tracking system, generating a social foraging network of birds' co-occurrences at the feeders. Next, we generated a "song similarity matrix" between all males in both aviaries. We then combined these data to test three, not necessarily mutually exclusive, predictions drawn from previous studies: (1) in contrast to control juveniles, corticosterone-treated juveniles will avoid copying their father's song (the "tutor choice hypothesis", based on [20]); (2) the more fathers and sons associate during the sensitive phase for song learning, the more similar the sons' songs will be to those of their fathers (the "social preference hypothesis", based on [42,43]) and (3) corticosterone-treated juveniles will not be capable of copying their father's song as accurately as control juveniles (the "cognitive impairment hypothesis", based on [26]).

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136 METHODS

137 *Breeding protocol and corticosterone treatment*

As described in [19], we housed 24 domesticated adult zebra finch pairs in breeding cages and of these, 13 pairs produced fertile eggs. To facilitate chick age-standardized hormone treatment we

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140 synchronised the within-brood hatching dates by replacing eggs with plastic dummies until the
141 brood was complete. Half of the chicks in each brood were assigned to the corticosterone (CORT)
142 treatment following [44]: between days 12 and 28 post-hatching, they were pipette-fed 20µl of
143 CORT (Sigma Aldrich; 0.155 mg/ml in peanut oil) twice daily, giving a total dose of 6.2 µg CORT/day.
144 This dose is known to result in plasma CORT levels comparable to those naturally induced in
145 untreated zebra finch chicks exposed to an acute stressor [44]. Control chicks were fed 20µl of pure
146 peanut oil when their siblings received CORT. For additional details, please see the Electronic
147 Supplementary Materials.

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149 *Social networks in aviaries*

150 When chicks were on average \pm SD = 35 \pm 1 days old (range: 33-38 days), we fitted them and their
151 parents with Passive Integrated Transponder (PIT) tags (Dorset ID) attached to unique colour rings,
152 and released families together into one of two identical indoor aviaries (3x3.1x3.2m) on the same
153 day. The aviaries were visually and acoustically isolated from each other. Each aviary contained
154 seven (N=34 birds: 16 females, 18 males) and six families (N=29 birds: 14 females, 15 males),
155 respectively, and both aviaries were equipped with two identical transparent feeders (28x28x10cm)
156 containing *ad libitum* finch seed at all times, except during a 3-day novel foraging task experiment
157 (described in [20]) that was excluded from analyses here. Feeders were designed as enclosed seed
158 trays with two open access points, each fitted with RFID antennae (Dorset ID) to record the PIT tags
159 of zebra finches as they freely entered and exited the feeders. The only way for the birds to obtain
160 food was to visit these feeders. During a 5-day habituation period to the free-flying aviaries we
161 checked that all birds regularly visited the feeders and observed no aggressive interactions around
162 the feeder access points. All birds' feeder visits were subsequently logged for 33 days. From this
163 temporal data stream we extracted bouts of foraging activity using a well-established clustering
164 algorithm [45] to define groups of birds visiting the feeder around the same time. This clustering
165 algorithm generated estimates of flock feeding events lasting on average 290 seconds (2.5th

percentile: 0 s (when birds landed on the feeder entrance and immediately left again), 97.5th percentile: 610 s). We then calculated association strengths between each dyad of birds in each aviary as the number of observations of both individuals in the same foraging group divided by the number of observations of at least one individual in a foraging group (i.e. the “simple ratio index”, ranging from 0 = never observed at the same feeder together, to 1 = always observed together; see Supplementary Methods of [20] for more details) with the *asnipe* package Version 1.1.3 [46] in R [47]. The social network data can be freely downloaded from [48]. The three social network metrics we extracted as predictors of father-son song similarity were a) the father-son association strength in each of the 33 daily foraging networks [19]; b) the total number and strength of the father’s daily associations (i.e. “weighted degree”) with all other aviary members excluding the son, as a measure of father “gregariousness” (which could affect his popularity as a song tutor [42]), and c) the son’s weighted degree excluding the father (as a highly sociable son may be less likely to pay attention to, and thus copy, the father’s song). All social network metrics were calculated including both male and female associates, as this reflects their actual social environment and takes into account any influences that female associations may have had on the males’ song learning processes. Females were excluded only from the song metrics (see below) as female zebra finches do not sing.

183

184 *Song recordings*

Male zebra finches each learn one song motif, which is repeated several times to form a song. We recorded the songs of all 17 adult males that were present in the breeding cages when the first chicks started hatching. Only 13 of these males produced fledglings and were present in the aviaries (and thus network analyses), but we also analysed the songs of the unsuccessful breeders (N=4 males), as we could not exclude the possibility that their songs were picked up by fledglings in neighbouring breeding cages. Captive-reared zebra finches tend to learn and produce songs heard between 35 and 65 days post-hatching, but they can incorporate elements heard before or after this

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3 192 sensitive phase [32]. CORT-treated (N=12) and control male (N=8) juveniles' songs were recorded
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5 193 when juveniles were at least 100 days old (mean \pm SD = 103 \pm 2 days) and their songs had crystallized
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7 194 to become stereotyped (this is known to occur around day 90 post-hatching [49]). Males were
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9 195 induced to sing by presenting each with an unfamiliar female in a sound-attenuated recording room.
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11 196 For additional details, please see the Electronic Supplementary Materials.
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15 198 *Song analyses*
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17 199 We analysed to what extent the song motif of each juvenile male (recorded once they reached
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19 200 adulthood) matched those of the 19 other juvenile males and of all 17 adult males they were
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21 201 acoustically exposed to. We predicted that most learning would occur from the seven (aviary 1) or
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23 202 six (aviary 2) adult males that fathered the juveniles and/or were present in the same free-flying
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25 203 aviaries from post-hatching day 35 onwards. Song elements were compared using dynamic time
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27 204 warping (dtw) in Luscinia (<http://rflachlan.github.io/Luscinia/>). This method has previously been
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29 205 applied successfully to zebra finches and other songbird species [23,50,51] to measure broad-scale
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31 206 features of song organisation as well as copying accuracy. The resulting dissimilarity matrix between
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33 207 all possible pairs of song elements in the dataset served as the basis for comparisons between
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35 208 individuals' song motifs: for each pair of individuals, we found the best fit between each of one's
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37 209 song motifs and those of the other, and averaged these to generate a motif dissimilarity matrix. For
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39 210 each juvenile we then ranked all potential song tutors (i.e. other male juveniles and adults, giving
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41 211 ranks 1-36) according to their song dissimilarity scores. We inferred that the male with the lowest
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43 212 dissimilarity score to the focal individual's song, and thus the most similar song, was the main song
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45 213 tutor, and this individual was assigned rank 1. The individual with the most dissimilar song (i.e. the
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47 214 largest dissimilarity score) was assigned rank 36. These data can be found in Supplementary Dataset
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49 215 1: Song Similarity Scores. Figure 1 shows examples of high and low father-son song motif similarity,
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51 216 and the song analyses are described in more detail in the Electronic Supplementary Materials.
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218 STATISTICAL ANALYSES

219 To first determine whether there was a link between CORT treatment and juveniles' use of the
220 father as the primary song tutor, we conducted a generalised linear mixed-effects model (GLMM)
221 with binomial error structure. The response variable was whether the juvenile's father was his main
222 song tutor ("1") or not ("0"), the fixed effect was CORT treatment (=1, control treatment=0), and the
223 random effect was family ID.

224

225 Next, to determine whether CORT treatment and father and son's social foraging association metrics
226 during the sensitive phase for song learning correlated with father-son song similarity, we conducted
227 a linear mixed-effects model with father-son song dissimilarity score as the response variable. Fixed
228 effects were i) CORT treatment; ii) the strength of father-son association in each of the daily foraging
229 networks [19]; iii) the total number and strength of the father's daily associations (i.e. "weighted
230 degree") with all other aviary members excluding the son (to control for "father gregariousness"), iv)
231 the son's weighted degree excluding the father (to control for "son gregariousness"), and v) the
232 number of fledglings in the family (as brood size can affect social learning strategies [12]). We
233 included "family ID" as a random effect, as the 20 juvenile males came from 11 different families
234 (two of the 13 fathers in the aviaries produced only daughters). Previous studies where juvenile
235 males were kept in small song learning groups with a single adult male tutor suggest that the
236 number of male peers present can affect song similarity [52,53]. To test for a correlation between
237 number of male offspring and father-son song similarity, we used the exact same linear mixed-
238 effects model as described above, but replaced the number of fledglings in the family with number
239 of male offspring (as these factors were strongly correlated and so could not both be included in the
240 same model). To test whether CORT treatment was related to the strength of father-son
241 associations, we conducted another linear mixed-effects model: the father-son association in the
242 daily foraging networks was the response variable, CORT treatment was the fixed effect, and family
243 ID the random effect.

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5 245 Finally, to test whether CORT treatment was linked to overall song copying accuracy, we conducted
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7 246 a linear mixed-effects model, where the response variable was the song dissimilarity score between
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9 247 juvenile and first-ranked tutor (i.e. with the smallest dissimilarity score), the fixed effect was CORT
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11 248 treatment, and the random effect was family ID.
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15 250 All statistical models were constructed using the ‘lme4’ package version 1.1-11 in R. To calculate the
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17 251 significance of fixed effects involving network metrics, and account for the fact that individuals’
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19 252 social association metrics are not independent of each other, we used a null models approach
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21 253 [54,55]: we compared the “observed” test statistic, i.e. the coefficient of the slope from the linear
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23 254 mixed-effects model of the observed data, to the distribution of test statistics generated by running
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25 255 the same statistical model on 10,000 permutations of the observed social associations using the R
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27 256 package ‘asnipe’ version 1.1.3 [46]. These permutations maintain the same data structure as the
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29 257 data collected, and only incrementally swap single observations of two individuals occurring in
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31 258 different feeding bouts/flocks [54]. This approach thus maintains, and controls for, aviary ID, the
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33 259 number and ID of individuals in each aviary, the number of times individuals were recorded to visit a
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35 260 feeder, and the specific feeder they visited.
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41 262 RESULTS

42 263 *Link between corticosterone treatment and song tutor choice*

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45 264 We tested whether CORT-treated juveniles were less likely to copy their fathers’ song. We found no
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47 265 significant link between CORT treatment and primary song tutor choice (GLMM: slope \pm s.e. = -1.077
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49 266 \pm 1.066, z_8 = -1.010, p = 0.312). The majority of juveniles (12/20) sang songs most similar to their
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51 267 fathers’ (Table 1). Of the eight birds whose songs were most similar to those of alternative tutors, six
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53 268 were CORT-treated juveniles and two were control birds. However, the majority of these eight
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55 269 juveniles’ songs were most similar to brothers from the same brood, with the father generally
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second-ranked ("Father Rank: 2" in Table 1) after a brother. The three exceptions in terms of song tutor choice (with father ranked 5th, 15th and 23rd) were all CORT-treated juveniles (Table 1). These patterns, illustrated in Electronic Supplementary Materials Figure S1, suggest that in some cases CORT-treated juveniles might avoid their father as a song tutor. Replicating this study with a larger sample size would help establish how robust and biologically meaningful this pattern is.

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276 *Links between corticosterone treatment, social associations and father-son song similarity*

Father-son song similarity was strongly affected by the CORT treatment, with CORT-treated juveniles producing songs that were less similar to their fathers' songs than those of control birds (Table 2).

Father-son song similarity was also correlated with the strength of father-son social associations (Table 2, illustrated for each network day in Figure S2): the more often fathers and sons were at the same feeder at the same time (Fig.2: thicker lines), the more similar were their songs (Fig.2: redder lines). Further, the number and strength of associations between the father and all other aviary members (excluding the son) showed a negative correlation with father-son song similarity: the more gregarious the father (Fig. 2: larger circles), the less similar his son's song was to his. In contrast, the son's 'gregariousness' showed no significant correlation with father-son song similarity. Finally, father-son song similarity was related to brood size: the more fledglings (of both sexes), the more similar the songs of father and son(s). The number of male fledglings in each nest showed no significant relationship with father-son song similarity (Table 2). These results are robust to the removal of two outliers, except for the effect of brood size, which was no longer significant (see Electronic Supplementary Materials: Results & Table S1).

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The finding that CORT treatment was associated with reduced father-son song similarity, while father-son association strength increased it (Table 2), raises the question whether there might be a direct and negative link between CORT treatment and father-son associations: did CORT juveniles associate less with their fathers as compared to control juveniles? Our post-hoc exploration of the

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3 296 data suggested a weak but significant negative relationship between CORT treatment and father-son
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5 297 association strength that emerged when comparing the observed networks to their randomizations
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7 298 (linear mixed-effects model: slope \pm s.e. = -0.007 ± 0.009 , $t = -0.758$, $p_{\text{rand}} = 0.028$). That is, despite
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9 299 being fairly small, the slope parameter of our model was significantly more negative than expected
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11 300 by chance (i.e. although the confidence interval overlaps 0, the slope is outside the 95% range of
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13 301 slopes (-0.0060 to 0.0080) generated by the randomisation procedure; see [54] for a detailed
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15 302 explanation of how such patterns can arise). However, absolute father-son association strength
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17 303 differed only slightly between CORT- and control juveniles (CORT ($N=12$): mean \pm SD = 0.175 ± 0.042 ;
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19 304 control ($N=8$): mean \pm SD = 0.172 ± 0.046). These results should thus be interpreted as CORT-
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21 305 treated juveniles having weaker associations with their fathers *relative to their potential to associate*
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23 306 *given their social network.*
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28 308 *Link between corticosterone treatment and overall copying accuracy*
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30 309 When we expanded the analysis to include all primary song tutors, rather than just the father, we
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32 310 found no significant relationship between CORT treatment and overall song learning accuracy: when
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34 311 comparing the songs of juveniles to those of their most similar tutor (i.e. the tutor with the smallest
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36 312 song dissimilarity score; see Table 1), control and CORT-treated individuals did not differ in their
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38 313 song dissimilarity scores (linear mixed-effects model: slope \pm s.e. = 0.007 ± 0.013 , $t_8 = 0.554$, $p =$
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40 314 0.587). This finding suggests that corticosterone exposure did not impair juveniles' cognitive ability
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42 315 to learn songs accurately.
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47 317 DISCUSSION
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49 318 The aim of this study was to investigate song learning accuracy and tutor choice of juvenile zebra
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51 319 finch males in free-mixing populations, and the social and hormonal mechanisms that might shape
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53 320 these song learning processes. Our results support the "social preference hypothesis": we found that
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55 321 foraging associations between juveniles and their fathers were strongly correlated with their song
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322 similarity. This effect was modulated by early-life stress: young males treated with corticosterone
323 were slightly less strongly connected to their fathers than expected by chance, and on average their
324 songs were less similar to those of their fathers when compared to the songs of control males. Our
325 results shed light on the mechanisms by which elevated corticosterone exposure early in life might
326 have downstream effects on song learning: by modulating social preferences of juveniles and their
327 potential song tutors.

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329 Our results corroborate the results of two previous zebra finch studies showing positive correlations
330 between social associations and tutor-pupil song similarity in an aviary context [42,43], and suggest
331 that the apparent contrasts in tutor choice observed therein may have actually been the by-product
332 of differences in social association patterns. Similar positive correlations between social associations
333 and song or call similarity patterns have been observed in other species, both in captivity (e.g.
334 starlings (*Sturnus vulgaris*) [56]) and in the wild (e.g. song sparrows (*Melospiza melodia*) [57];
335 Campbell's monkeys (*Cercopithecus campbelli campbelli*) [58]).

336

337 We do not claim that our zebra finches were singing (and learning songs) inside the feeders. Instead,
338 our social foraging networks are more likely representative of birds' general social preferences
339 outside the feeders (i.e. by capturing correlations in their behaviour across the day), where singing
340 and song learning presumably occurred. Previous studies suggest that different types of social
341 networks (e.g. proximity vs. interaction networks) do not necessarily correlate [59] nor necessarily
342 concur in predicting information transmission [60]. Work is underway to quantify multi-context
343 social networks in zebra finches to assess the domain-generalizability of their foraging associations [61].
344 In addition, the development of light-weight microphone backpacks [62] offers the exciting
345 possibility of tracking vocal interactions and song development throughout the juveniles' sensitive
346 phase for song learning in a free-flying context, and thus map dynamic social association networks

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3 347 onto dynamic communication networks [63] rather than just the end-product of the crystallised
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9 350 In line with our previous study [19], our results provide greater insights into the effects of early-life
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11 351 corticosterone exposure on social preferences, in this case reducing father-son foraging associations.
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13 352 Further work tracking individual behaviour in finer detail [61] might be able to reveal the factors and
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15 353 their directionality underlying differences in the potential to associate, such as whether they are
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17 354 driven by the juveniles and/or the fathers. Although included primarily as a control variable, we also
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19 355 found that more gregarious fathers had sons with less similar songs. This could suggest that more
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21 356 gregarious fathers might be less preferred as song models, or perhaps that genetic factors that
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23 357 increase father gregariousness also somehow reduce son song copying accuracy. However, it seems
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25 358 more likely that such gregarious fathers create a more complex social and acoustic environment in
26
27 359 which accurate song copying is more challenging for their male offspring. A quarter of the sons were
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29 360 also found to have songs most similar to those of their brothers. This could indicate horizontal social
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31 361 transmission of song, a phenomenon previously described amongst juvenile peers in small flocks of
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33 362 captive zebra finches containing a single adult song tutor [64]. Alternatively, brothers might not
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35 363 necessarily copy each other's songs directly, but show similar song learning tendencies (e.g. they
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37 364 may, genetically and/or through early-life effects, be predisposed to attend to the same cues in their
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39 365 (social) environment, as seen in mouse sibs [65]), resulting in more similar songs indirectly. It is
40
41 366 impossible to distinguish between these hypotheses without further experimental manipulation.
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43 367 Selective feeders, perches or roosting sites (see e.g. [66]) could be used to manipulate the
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45 368 gregariousness of fathers as well as father-son and peer bonds, and help to elucidate the potential
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47 369 causal links between social associations/preferences and song learning patterns.
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53 371 Similar to the pattern we previously observed in the context of socially learning to solve a novel
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55 372 foraging task [20], some corticosterone-treated sons appear to have sought out song tutors other

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3 373 than the father. This could be because the father may not have been preferred as a role model due
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5 374 to the negative early-life experiences of the corticosterone-treated offspring in the nest, which
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7 375 would support the “tutor choice hypothesis”. Alternatively, fathers may have differentially
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9 376 interacted with corticosterone-treated and control sons, for example because they perceived their
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11 377 corticosterone-treated sons to be of lower quality; corticosterone-treated juveniles weighed less
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13 378 than control juveniles at the end of corticosterone treatment just before fledging ([19]
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15 379 Supplementary Materials) and fathers may have noticed this. We hope that recent developments in
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17 380 tracking techniques [61] will help to determine the directionality of this effect (father to son versus
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19 381 son to father) in the future.
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23 383 Previous studies have suggested that developmental stress may hamper the *ability* of birds to learn
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25 384 their songs accurately [67,68] (although see [69,70]). However, our findings suggest that
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27 385 corticosterone-induced changes in social preferences, rather than an impaired cognitive ability,
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29 386 could help explain some of the reported tutor-tutee song (dis)similarities. Our results show that
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31 387 corticosterone-treated juveniles copied their most similar model song as accurately as the control
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33 388 juveniles copied theirs. Similarly, our previous study on the same birds showed that corticosterone-
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35 389 treated juveniles were faster, not slower, to learn to solve a novel foraging task as compared to the
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37 390 control juveniles [20], as has also been found in another zebra finch population that controlled for
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39 391 foraging motivation through quantifying metabolic rate [71]. Our findings thus appear to provide no
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41 392 support for the “cognitive impairment hypothesis” in our specific study population (although this
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43 393 could be a false negative (i.e. type II error) due to small sample size), and suggest that stressors may
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45 394 influence song development indirectly as a consequence of their effects on social preferences. Thus,
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47 395 our study has opened up a new window through which to explore the hormonal and behavioural
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49 396 mechanisms underlying information acquisition (i.e. tutor choice) and use (i.e. copying accuracy) in
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51 397 song learning. Unfortunately, our study does not allow us to completely disentangle the intertwined
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53 398 influences of corticosterone exposure and social preference patterns [19] on song learning due to
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399 our limited sample size. In addition, chick sex was unknown at the start of the corticosterone
400 manipulation, resulting in several broods without control sons. However, our findings provide a
401 useful context to, and help to elucidate the contrasting results of previous studies. As a result, we
402 are starting to develop a deeper understanding of factors underlying song learning outcomes.
403
404 Stressors experienced early in life clearly affect juveniles' social learning strategies, both when
405 learning about novel food sources [12,20] and when learning about song (current study). Here, by
406 integrating social and communication networks [63], we suggest that changes in social preferences
407 could play a key role in modulating song learning by juveniles; young males that had strong social
408 bonds with their fathers expressed more similar songs. The functional significance and ecological
409 relevance of juveniles (not) copying their fathers' songs has remained unclear. Most songbirds
410 acquire their songs after dispersing from their natal territory, learning from males other than their
411 fathers, with some species learning during an early critical period, while others continuing to learn
412 throughout life [24]. It has been suggested that learning from the father in early development may
413 facilitate later kinship recognition and inbreeding avoidance in wild zebra finches, where extended
414 breeding seasons and high mortality lead to high rates of re-pairing in the colonies [40]. But if a male
415 was successful in producing offspring, why would any of his sons, even if stressed in early
416 development, decide *not* to copy him? Our study suggests that inaccurate/not copying of the
417 father's song may not be a directed strategy by juvenile males, but instead could be a by-product of
418 other social processes. Our findings, when combined with previous studies, clearly highlight the
419 importance of social preference patterns in modulating song learning, and ultimately the links
420 between early-life conditions, social affiliations and information use.

421 ETHICS

422 All experiments were approved by the local animal ethics committee of the University of St. Andrews
423 (Scotland) and the experiments were conducted in accordance with the Home Office Animals
424 (Scientific) Procedures Act 1986 under project licence no. 60/4068 held by KAS and personal licence
425 no. 60/13491 held by NJB.

426

427 ELECTRONIC SUPPLEMENTARY MATERIALS

428 Methodological details, additional analyses and results have been uploaded as part of the electronic
429 supplementary material.

430

431 DATA ACCESSIBILITY

432 The social network data as first reported in [19] are publicly available via
433 <http://datadryad.org/resource/doi:10.5061/dryad.7qs06>

434 The complete song similarity data and a song-network data summary file have been uploaded as
435 Supplementary Datasets 1 and 2, respectively, and will be published with this manuscript.

436

437 COMPETING INTERESTS

438 We have no competing interests.

439

440 AUTHORS' CONTRIBUTIONS

441 NJB, KAS, and CNT designed the study. NJB collected the data, RL analysed the songs, NJB, DRF and
442 RL planned the statistical analyses and DRF conducted the analyses and created the figures. NJB and
443 DRF wrote the paper with significant input from all co-authors.

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FIGURE LEGENDS

Figure 1. Example songs. The top two panels (a and c) are father songs, and the lower two panels (b and d) are their sons' songs, respectively. a)-b) illustrate a high father-son song similarity (the father's song was the top-ranked model), while c)-d) illustrate a very low song similarity (the father's song was ranked 23rd in similarity to the son's song).

Figure 2. The social foraging associations and song similarities of the males in each of the two aviaries. Our social network metrics and analyses included all males and females in the aviaries, but for the purposes of illustration only males are drawn here, as female zebra finches do not sing. Numbers represent family ID. This figure illustrates that fathers (black circles) and sons (grey circles: controls; with red outline: CORT-treated) with stronger social associations (thicker lines) had more similar songs (redder lines), while more gregarious fathers (larger circles) generated less similar songs in their pupils (blue-er lines).

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661 **TABLES**

662 **Table 1. Song tutor choice of control and corticosterone-treated juveniles.**

	Primary song tutor			
Juvenile treatment	Father	Not Father ^a	Father Rank	Relation to tutor with most similar song
Control	6	2	2, 2	brother, unrelated adult
Corticosterone	6	6	2, 2, 2, 5, 15, 23	brother, brother, brother, unrelated peer, brother, unrelated adult

663 ^aShaded cells refer to juveniles whose songs were not most similar to their fathers’.

664 The 4th column shows which song-similarity rank the father’s song occupied, and the final column

665 shows whom these juveniles copied primarily instead.

Table 2. Effect of corticosterone (CORT) treatment and social associations on father-son song dissimilarity scores. Full linear mixed-effects model results (N=13 fathers, 20 sons). P values are calculated by comparing the observed slope coefficients with the distribution of slope coefficients from 10,000 permutations of the social network data. Hence P values do not always exactly match the t-statistic (which is a parametric estimate that depends on sample size, which is not defined for social network data). For each fixed effect, the first row of values was generated by the full model, and the second row represents results of the full model but including number of male offspring instead of number of fledglings for each zebra finch family. Values in bold indicate significant predictors in both models.

Fixed effects	Slope	SE	95% range of random coefficients	t	P _{rand}
Intercept	0.2257	0.0223		10.115	
	0.1981	0.0229		8.645	
CORT treatment	0.0234	0.0030	0.0227 to 0.0230	7.803	0.016
	0.0234	0.0030	0.0230 to 0.0232	7.777	0.003
Father-son association	-0.0346	0.0171	-0.0308 to 0.0221	-2.017	<0.001
	-0.0342	0.0172	-0.0284 to 0.0011	-1.992	0.011
Father gregariousness	0.0031	0.0012	0.0008 to 0.0030	2.545	<0.001
	0.0031	0.0012	0.0016 to 0.0027	2.530	0.001
Son gregariousness	-0.0020	0.0010	-0.0023 to -0.0014	-1.981	0.72
	-0.0020	0.0010	-0.0021 to -0.0016	-1.972	0.292
Number of fledglings	-0.0121	0.0061	-0.0125 to -0.0122	-1.973	<0.001
Number of male offspring	-0.0067	0.0111	-0.0069 to -0.0067	-0.605	0.575
Random effects	Variance	SD	% total		
Family	0.0007	0.0259	47.34%		
	0.0009	0.0305	55.50%		

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